TILAPIINE FISHES FROM CRATER-LAKES NORTH OF LAKE MALAWI

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SYNOPSIS

Tilapia chungruruensis Ahl of a crater-lake in the Rungwe Mountains, about 32 km north of Lake Malawi, is redescribed from the holotype and ten of the 'cotypes' (paratypes). The population is related to the *Sarotherodon squamipinnis* group of Lake Malawi. The holotype cannot be assigned to any of the four species of this group, nor to the related species of Lakes Mweru and Rukwa, and consequently the name of neither of these can be regarded as its synonym. It may represent the result of hybridization, although this cannot be definitely assumed. Some of the 'cotypes', however, are probably *S. lidole* (Trewavas) modified by the environment.

Changes in the level of Lake Malawi may have permitted the natural populating of the crater-lake or it may have been stocked by man. All the specimens have relatively bigger heads than their Lake Malawi relatives and are sexually mature at a much smaller size. A comparison is drawn with the *Sarotherodon* species of a crater-lake in West Cameroon and with isolated populations of other species.

Lake Tschungruru is probably the same lake as that now known as Masoko. Two specimens of *S. lidole* from Lake Kingiri, a crater-lake nearer to Lake Malawi, are also described.

INTRODUCTION

The main object of this paper is to redescribe the types of *Tilapia chungruruensis* Ahl, 1924, and to relate them to other tilapiine fishes of the genus *Sarotherodon* (formerly subgenus) to which they belong. I have also considered two specimens of this genus collected by Dr H. Albrecht in Lake Kingiri, north of Lake Malawi, and some juveniles collected in Lake Masoko by Miss C. K. Ricardo (later Dr Ricardo-Bertram) in 1937.

I have been privileged to examine the holotype and eleven of the twenty-nine 'cotypes' (paratypes) of *T. chungruruensis*, thanks to the kindness of Dr K. Deckert, who was in charge of the fish collections in the Berlin Museum at the time of the loan.

The meristic characters, the black colour and tasselled genital papilla of the males, the long pectoral fin, the long, slender caudal peduncle and the shape of the lower pharyngeal bone collectively relate these fishes to the Malawi species-flock of the *S. squamipinnis* group and distinguish them from *S. rukwaensis* and *S. macrochir*, tasselled *Sarotherodon* of neighbouring basins. At the time of Ahl's description and Ricardo's determination the four species of the Malawi group had not been distinguished. On the same morphological criteria used for the Malawi group (Trewavas, 1941 ; Lowe, 1952) I find that the holotype and two of the paratypes of *S. chungruruensis* belong to one species, not exactly identifiable with either of the Lake Malawi species, eight others to a second species which I identify with *S. lidole*. (The eleventh 'cotype' is a juvenile of 42 mm SL, too small to be determined.) I

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therefore describe them under two headings, grouping the Lake Masoko juveniles tentatively with *S. chungruruensis* and the Lake Kingiri specimens with *S. lidole*.

DESCRIPTION OF THE LOCALITIES

Ahl (1924) quoted Fülleborn's account of the Tschungruru-See. He stated that it is the Kiungvuvu of Cross, near the mission station of Neu-Wangermannshöhe. This name is not found on recent maps, but in the *Atlas* of Stuhlmann's *Deutsch Ost-Afrika* it is marked at 9°17′S, 33°50′E, north of Lake Malawi but within its drainage basin. The crater-lake Masoko lies a few kilometres NW of this at about 9°16′S, 33°43′E and is probably the same lake under another name.

Fülleborn described Lake Tschungruru as a crater-lake about 500 m in diameter and 45 m deep with no surface outlet. The water did not taste brackish.

Lake Kingiri is a crater-lake about 8 km north of Lake Malawi and 3 km north of Ipinda Ferry.

DESCRIPTION OF SPECIES

Sarotherodon chungruruensis (Ahl)

Tilapia chungruruensis Ahl, 1924 : 86.
Tilapia squamipinnis (part., nec Günther ?) ; Ricardo, 1939 : 655.

Type material. Holotype : the 'type' by original designation is the largest specimen, a mature male of total length 193 mm (153+40 mm), one of thirty numbered 208 in the Zoological Museum of the Humboldt University, Berlin, collected by Professor Fülleborn about 1923 in Lake Tschungruru, a crater-lake in the Rungwe Mountains, north of Lake Malawi.

Lectoparatypes :[1] two specimens, respectively 51 and 69 mm in SL. I assign the eight other 'cotypes' examined to *S. lidole* (p. 151).

Description. Some of the variation is consistent with the usual allometries, so that the highest ratios for depth of body, length of snout, depth of preorbital, interorbital width and length of jaw are those of the holotype. So also is that of head-length, a less usual trend, but found also in some other phytoplankton feeders (*S. linnellii* and *S. caroli* of Lake Barombi-Mbo, Cameroons), and the length of the pectoral fin. The eye, as usual, is negatively allometric.

Proportions as % SL : depth of body 37·6–38·5 ; length of head 37·3–40·5 ; length of pectoral fin 35–42 ; length of caudal peduncle 13·8–16·0 (1·15–1·3 times its depth).

Proportions as % length of head : snout 29–38 ; eye 29·0–20·5 ; depth of preorbital 16·8–24·2 ; interorbital width 31·6–39·7 ; length of lower jaw 32, 32·8 in the small specimens, 39 in the holotype.

Teeth in 3–4 series in upper jaw, 4–5 in lower ; 42–78 in outer row of upper jaw ; with slender shafts and curved crowns, the outer bicuspid in the young,

[1] Since the holotype is not a lectotype I think that this, and not 'paralectotypes' is the correct title for those 'cotypes' that I recognize as conspecific with the holotype.

mixed bi- and tri-cuspid in the holotype, which has many of the crowns broken off ; inner tricuspid, but also many of these are broken in the holotype.

Gill-rakers on first arch 2+1+17.

Lower pharyngeal bone : see Tables 1 and 2 and Pl. 3.

Scales in 2 or 3 series on the cheek ; 32 in the lateral line series, 4 or 4½ from origin of dorsal to lateral line.

Dorsal XIV 12 (holotype), XV 11 or XV 12. Anal III 10–11. Caudal truncate or very slightly emarginate, not densely scaled, but with small scales extending part-way along upper and lower rays.

Genital papilla small in young ; in the holotype with several short branches arising in two groups from a club-shaped base.

Vertebrae 30 (14+16) in the holotype and one other.

Colour. The holotype, a ripening male, is dark all over, including the fins. The colour is now dark brown, probably faded from black. Even the dorsal lappets are now dark. The 69 mm specimen is pale, without markings, the vertical fins faintly dusky. In the 51 mm specimen the dorsal fin and back are dark ; along the middle of the flank are four dark spots produced vertically.

Additional specimens. Four young of 35·5–61·0 mm SL were collected in crater-lake Masoko in 1937 by Miss C. K. Ricardo (later Dr Ricardo-Bertram). These also belong to the *S. squamipinnis* group and both jaws and pharynx are too well toothed for *S. lidole*. There are 32 or 33 scales in the lateral line series, 8 or 9 soft rays in the anal fin, 17 or 18 gill-rakers on the lower part of the first arch. The dorsal formula is XV 10 (f.1), XV 11 (f.2) or XVI 10 (f.1). The three of 56–61 mm have 4–5 rows of teeth in the upper jaw, 5–6 in the lower ; the length of head is 36% SL. There are 6 dark vertical bars on the body, accentuated above the lateral line.

We have not so far succeeded in distinguishing between the four Malawi species at such a small size and in placing these in *S. chungruruensis*. I am merely indicating that like the types they are not *S. lidole* and may be one of the other species or the result of hybridization between some of them.

Sarotherodon lidole (Trewavas)

Tilapia lidole Trewavas, 1941 : 297 ; Bertram, Borley & Trewavas, 1942 : 34, fig. 4C & D ; fig. 6C ; Lowe, 1952 : 2–65.

Description (of eight specimens from Lake Tschungruru and, in brackets, two from Lake Kingiri).

The Tschungruru specimens are eight of the paratypes of *T. chungruruensis*, nos 2 and 4–10 in Table 1. The two Kingiri fishes measure 139+31·5 and 162+39 mm to the end of the middle caudal rays ; they are listed at the end of Table 1.

Proportions as % SL : depth of body 34·8–40·0 (40·5, 38·4) ; length of head 39·4–42·4 (38·5, 38·6) ; length of pectoral fin 38·0–43·3 (41·5, 40·0) ; length of caudal peduncle 15·3–16·8 (16·3, 15·7) ; length of lower jaw 11·6–14·8.

Depth of caudal peduncle contained 1·27–1·5 times in its length.

Proportions as % length of head : length of snout 34·2–39·0 (32·6, 26·8) ; diameter of eye 21·3–24·4 (24·2, 21·0) with no evidence of allometry ; depth of preorbital 18·7–23·8 (22·4) ; interorbital width 34·0–44·5 (45·2, 44·7) ; length of lower jaw 27·8–39·6 (31·8–32·3).

Proportions of lower pharyngeal bone : see Tables 1 and 2. Pharyngeal teeth very fine, in a restricted area.

Teeth in 3 rows in both jaws with an incomplete fourth in a few ; with long, slender shafts and expanded crowns ; those of outer row bicuspid in small specimens, in some bigger fishes with an admixture of tricuspid and occasionally a few unicuspid, often but not always by wear ; a few posterior often simple. Teeth of inner rows tricuspid unless with worn crowns. Number of outer teeth in upper jaw 52 at SL 65·5 mm, 70–82 from 86 to 162 mm.

Gill-rakers 2–4 + 1 + 17–20 on first arch.

Scales on cheek in 2–3 rows, occasionally a few small scales of a fourth row ; lateral line series 33–34 ; 4, 4½ or 5 from origin of dorsal fin to lateral line, about 20 around caudal peduncle.

Dorsal XIV–XV 10–11 (XVI 11, XVII 10 in Lake Kingiri) ; anal III 8–10.

Vertebrae 31 in three counted.

Genital papilla of a male of SL 143 mm large, with two groups of short papillae at its distal end, the pore between them. A female of SL 123 mm has enlarged ovaries, in which the biggest egg is 3 mm in long diameter.

TABLE 1

Data from the holotype and ten paratypes of *Sarotherodon chungruruensis* (Ahl) in order of size

No. of specimen	SL (mm)	Head % SL	Ph.l. % head	Ph.w. % head	Ph.l/w	Ph.bl./dent.	Rows teeth in lower jaw
1.	**51**	**37·3**	**31·6**	**31·6**	**1·0**	**1·3**	**4–5**
2.	65·5	40·7	36·3	26·2	1·4	1·8	3
3.	**69·0**	**37·7**	**34·6**	**32·7**	**1·06**	**1·2**	**4**
4.	86·0	42·0	36·4	27·8	1·3	2·5	3
5.	93·5	40·6	37·0	26·3	1·4	2·06	3
6.	123·0	39·4	37·5	26·0	1·4	3·4	3
7.	125·0	42·4	39·6	27·0	1·47	3·88	3
8.	126·0	40·8	34·0	25·6	1·32	3·4	3
9.	141·0	40·4	38·0	25·0	1·5	3·0	3–4
10.	143·0	39·6	40·7	28·6	1·42	2·7	3
11.	**154·0**	**42·5**	**35·5**	**28·6**	**1·24**	**1·4**	**4–5**
LAKE KINGIRI							
	139·0	38·5	37·6	27·2	1·38	1·88	3
	162·0	38·6	36·0	26·2	1·37	2·2	3

No. 11 is the holotype and nos 1 and 3 resemble it in the proportions of the lower pharyngeal bone and number of rows of teeth in the jaws ; data for these are in bold type. The other specimens are determined as *S. lidole*. The measurements of the lower pharyngeal bone are its median length (Ph.l.), greatest width (Ph.w.), both expressed as % length of head ; the median length divided by the width (Ph.l/w.) and the length of the anterior blade divided by the median length of the dentigerous area (Ph.bl./dent.). For comparison the same data are given for two specimens of *T. lidole* from Lake Kingiri.

TABLE 2

Summary of Table 1

	S. chungruruensis holotype and lectoparatypes (Specimens 11, 1 and 3)	Other 'cotypes', determined as *S. lidole* (Specimens 2, 4–10)	Two *S. lidole* from Lake Kingiri
Ph.l. % head	31·6–35·5	34·0–40·7	36·0, 37·6
Ph.w. % head	28·6–32·7	25·6–28·6	26·2, 27·2
Ph.l./w.	1·0–1·24	1·3–1·5	1·37, 1·38
Ph.l./dent.	2·2–2·4	2·8–4·8	2·8, 3·2

TABLE 3

Pharyngeal proportions in Lake Malawi

	S. lidole	*S. squamipinnis* and *S. saka*	*S. karongae*
N	12	5	4
SL (mm)	230–285	200–250	150–235
Phar.l./w.	1·33–1·47	1·22–1·38	1·29–1·35
Phar.l./l.dent.	3·0–4·5	2·4–3·1	2·16–2·25

Colour. Small specimens and females with five dark blotches, vertically drawn out, along the side and some with two fainter on the caudal peduncle; vaguer markings in a more dorsal row; one male almost uniformly dark. Males with broad dark margin on dorsal fin and dark anal fin, in one with narrow white margin (as preserved). Females with no marginal dorsal band. Smaller specimens with a tilapia-mark.

Caudal clear in small specimens; in mature males of Lake Tschungruru dark or dusky with a white margin or upper corner. Male of Lake Kingiri with caudal dark proximally, distally with a dark reticulum and a pale margin.

COMPARISON WITH SPECIES OF LAKE MALAWI

S. lidole

1. *Resemblances*

I have identified eight Tschungruru specimens with this species because of the proportions of the pharyngeal, the narrow bands of teeth in the jaws and the general shape.

(a) Pharyngeal. In adults of Lake Malawi, all bigger than the crater-lake specimens, the median length of the pharyngeal bone is 1·38–1·5 times its greatest width. In the crater-lake the ratio is 1·3–1·5 (Tables 1 and 2), including specimens down to 65·5 mm SL, thus smaller than the sizes at which the species has been recognized in Lake Malawi. The dentigerous area is restricted and the blade is long, also characters distinguishing *S. lidole*.

(b) Jaw teeth. The inner teeth of the jaws are set in irregular rows and the formula '3–4', including the outer row, expresses this irregularity rather than variation within the size-range of the crater-lake sample. In Lake Malawi, even in the much bigger adults, 3–5 is the range, in contrast to 4–7 in *S. saka*, *S. squamipinnis* and *S. karongae*.

(c) Plates 1 and 2 show the characteristic position of the greatest depth of body in front of the dorsal fin in contrast to the other species.

2. *Differences from the Malawi population*

(a) Length of head. *S. lidole* in Lake Malawi is credited by the fishermen with a big head and the ratio there shows a higher range, though with a wide overlap, in comparison with that of the other species. It is 34·0–38·5% SL in Lake Malawi in contrast to 39·4–42·4 in the crater-lake. It is true that the Malawi specimens are bigger, but smaller Malawi fishes of indeterminate species, probably including *S. lidole*, have head ratios in the lower part of the range. The biggest ratios are found in much bigger, mature fishes. The significance of this will be discussed below.

(b) Size at sexual maturity. Lowe (1952 : 24) gives the minimum size at sexual maturity for both males and females of *S. lidole* as 28 cm TL (about 240 mm SL). In contrast, the crater-lake male of SL 143 mm (TL about 17·5 cm) already has an enlarged genital papilla terminating in a short tassel, and a female of SL 123 mm (TL 15 cm) has an ovarian egg of 3 mm long diameter.

The small size and early age of sexual maturity in pond populations of other species of *Sarotherodon* are well known (Lowe, 1955 : 365 ; 1958 ; Hickling, 1962, 1963).

In the other crater-lake, Kingiri, the two available specimens have a head ratio at the upper end of the Malawi range. Their gonads were removed, but a short tassel on the papilla of the male shows that here too sexual maturity occurs at a smaller size than in the Great Lake.

S. chungruruensis

The holotype contrasts with the *S. lidole* of the same crater-lake in the shape of the pharyngeal bone as expressed in its length : width ratio as well as the bigger dentigerous area relative to the length of blade (Pl. 3 and Table 2). It also has more rows of teeth in the jaws and that this is not only because of its greater size is confirmed by the small lectoparatypes, which also combine a wider tooth-band with a general shape contrasting with that of *S. lidole* (Pls 1 and 2).

The pharyngeal bone of the holotype contrasts more with that of the *S. lidole* of Lake Tschungruru than with those of Lake Malawi as figured by Bertram *et al.* (1942, fig. 6C). Column B of that figure, labelled *T. squamipinnis*, includes pharyngeals also from *S. saka* (Lowe) (at that time not recognized as distinct), but from what we now know of *S. saka* these would be the pharyngeals with the broadest dentigerous area, and those with a concave-sided dentigerous area would be *S. squamipinnis*. It is the latter that most resemble the pharyngeals of *S. chungruruensis*, but the breeding male of *S. squamipinnis* is pale blue with a white head, that of *S. saka* black, as *S. chungruruensis* must have been.

The character of the pharyngeal bone may well have changed in the environment of the crater-lake, so this is not a final argument for not identifying *S. chungruruensis* with *S. saka*. The holotype (and indeed some of the others) may have been the result of hybridization between, for example, *S. saka* and *S. lidole*.

SIGNIFICANCE OF THE BIG HEAD

Not only is there a high head : body ratio in the *S. lidole* of the crater-lake, but the same ratio in the type and lectoparatypes of *T. chungruruensis* is in the highest part of the range for all the species of this group in Lake Malawi.

Big heads have been found in small populations of other species of *Sarotherodon*. Two lagoon populations of the type species, *S. melanotheron*, have head ratios ranging higher than the range for the rest of this widespread species. The type specimens of *S. niloticus eduardianus* occupied a small crater-lake on the lower slopes of Ruwenzori, near enough to the shore of Lake George to have received its fish population from that lake during an exceptionally wet season. They had evidently become more crowded as time went on and when caught were stranded on the shore of the shrinking lake. Their head-ratios ranged from 36·6 to 39·8% SL, nearly all greater than in the parent population. The *S. niloticus* in Buhuku Lagoon when it was temporarily isolated from Lake Albert (see Lowe, 1958) had head-lengths ranging from 36·4 to 41·0% SL in contrast to 34·3 to 39·6% in a sample of comparable size from the open lake. The *S. niloticus vulcani* of Crater-lake A on the central island of Lake Rudolf provide a further example. Most of the endemic cichlid species of the Cameroons crater-lake, Barombi Mbo, are characterized by big heads, and *S. linnellii* and *S. caroli* provide an interesting parallel to *S. lidole* and the rest of the Malawi species-flock, both structurally and ecologically (Trewavas *et al.*, 1972).

The relative growth phenomenon resulting in a big head is known in pisciculture in the 'hunger-form' of the common carp.

THE ORIGIN OF THE TSCHUNGRURU (?=MASOKO) FISH POPULATION

Dixey (1926) gives the evidence for previous surface levels of Lake Malawi. The level has been falling since the Tertiary, for which epoch two levels have been determined, respectively 300 m and 210 m above the present level. The fall is attributed mainly to subsidence of the rift floor. The Tertiary lake consisted only of the northern part, which extended from about 32 km to the north-west of the present northern end to about the latitude of Deep Bay (10°24'S). During the Quaternary the lake extended southwards and when it was 120 m above its present level still included an area 80 km north of the present north end.

Just where the limit was at the time, relatively recent, of the volcanic activity that produced the Rungwe Mountains, including the Masoko crater, is not certain, but it seems quite possible that it was near enough to be supplied naturally with its fish fauna from Lake Malawi or one of its affluent rivers.

If it was stocked by man the source would be the same, namely the fry that abound among the grasses and reeds of the banks ; they might have survived a journey of at the most 30 km in a calabash or a cool clay pot.

Lowe (1952, 1953) has described the breeding places, seasons and colours that characterize the three tasselled tilapias of the Malawi flock at the south end of the lake. Her stay of one month (March) at Karonga near the north end was not long enough to establish such distinctions, and she found there some specimens that

seemed 'equivalent to *T. squamipinnis* and *T. saka* at the south end of the lake', that is to a single representative of these two species, as well as some that could be assigned to each of them. The northern species, *S. karongae*, was also present and there was evidence that *S. lidole* was caught at a different time of the year (October).

None of the examined types of *S. chungruruensis* has a pharyngeal bone big enough for *S. karongae* so that the source-species must be *S. lidole* and one or both of the other two.

The seasons and topography in the north of Malawi do not provide the same framework as that within which the three southern forms preserve their identity. Still more is this true of Lake Masoko and although *S. lidole* has kept its characteristics with but slight modification, I find it impossible to be sure that *S. chungruruensis* is identical with either *S. squamipinnis* or *S. saka*, or to justify the synonymizing of its name with either the older *S. squamipinnis* or the junior *S. saka*. It seems more expedient to retain the name *chungruruensis* for the section of the crater-lake population that may be a hybrid between two or more of the southern species or a modified population of *S. saka*, and to refrain from suppressing the latter name in favour of that of such a doubtful form.

A fresh examination of the Lake Masoko population and its ecology with these possibilities in mind would be interesting. The specimens collected by Ricardo in 1937 are too young to provide evidence, but they do show that fish were still in the lake at that time.

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